

An Ecological Study  
of Two Sympatric Species of *Fasciolaria*  
(Mollusca : Gastropoda)  
in Alligator Harbor, Florida<sup>1,2</sup>

BY

FRED ETHAN WELLS, Jr.

Department of Biological Science, The Florida State University, Tallahassee, Florida 32306

(1 Plate; 9 Text figures)

## INTRODUCTION

TWO SPECIES OF TULIP SHELLS, *Fasciolaria hunteria* (PERRY, 1811), the banded tulip, and *F. tulipa* LINNAEUS, 1758, the true tulip, occur along the southeastern coast of the United States. These species are members of the neogastropod family Fascioliidae and are found from Beaufort, North Carolina, on the Atlantic coast southward to southern Florida. Their distribution then follows the Gulf of Mexico westward to Texas, where *F. distans* LAMARCK, 1847, replaces *F. hunteria*. *Fasciolaria tulipa* ranges southward along the Mexican coast and is found throughout the Caribbean Sea. Both *F. hunteria* and *F. tulipa* are present locally in Alligator Harbor, Franklin County, Florida. Another member of the Fascioliidae, the horse conch, *Pleuroploca gigantea* (KIENER, 1840) is present but is not included in the present study. Except for the taxonomic descriptions, little is known about either species. Until recently they were thought to be of no commercial importance, but in a report on prey selection H. WELLS (1958) found *F. hunteria* to be a predator of the commercially important Virginia oyster, *Crassostrea virginica* (GMELIN, 1791). *Fasciolaria hunteria* prefers the drill *Urosalpinx cinerea* (SAY, 1822) as a prey species over the Virginia oyster (H. WELLS, *op. cit.*), and thus could be

important in decreasing oyster predation by the drills. In a previous study of oyster predators in Alligator Harbor, MENZEL & NICHY (1958) did not discuss *F. hunteria*.

The theoretical problems arising from a sympatric distribution of two closely related species make the biology of *Fasciolaria hunteria* and *F. tulipa* fertile ground for investigation. This study was undertaken to analyze the habitats, population structure, mating habits, predators, escape responses, and aspects of the anatomy of the two species in relation to the mechanisms that allow them to live sympatrically.

## MATERIALS AND METHODS

Observations of *Fasciolaria hunteria* and *F. tulipa* were made both in the field and in the laboratory from January to April, 1969. Laboratory experiments were intended to supplement the field observations rather than substitute for them. Population studies were conducted along the docks of the old Florida State University marine laboratory and along the southern portion of the Bay Mouth Bar. All individuals found in these areas were measured, marked, and returned to the site of collection. Measurements of length and width of individuals less than 130 mm long were made with a steel caliper to the nearest 0.1 mm, while individuals over 130 mm long were measured with a wooden ruler to the nearest 1 mm. Marking was done initially in the manner described by HATHAWAY (1957). A file was used to scrape incrustations and the periostracum off the body whorl of the shell. Plastic model airplane paint, which dries in about 10 minutes, was used to num-

<sup>1</sup> Presented to the Department of Biological Science, The Florida State University in partial fulfillment of the requirements for the degree of Master of Science. This research was supported by a Graduate Traineeship granted by the National Science Foundation.

<sup>2</sup> Present address: Department of Zoology, McGill University, Montreal, Canada

ber the shells, after which the animals were returned to the collection site. After it became apparent in both the field and in the laboratory that the paint would flake off certain individuals, subsequent markings were made by notching the lip of the shell with a file. This method of marking fails to maintain a differentiation of individuals but variations in the number and location of notches were used on different trips. The notch is permanent and can be identified on the old lip even after the shell has grown.

Physical data recorded on each collecting trip included date; collecting times; time and depth of low tide; salinity; temperatures of sand, water, and air; water and general atmospheric conditions. Salinities were determined by using the titration method described by STRICKLAND & PARSONS (1960). Because of the extreme difficulty of locating individuals in several feet of water, most collecting was done at low tide.

Salinities in the laboratory aquaria varied from 32.7 to 37.4 parts per thousand, and temperatures varied from 13.5° C to 21.0° C. Salinities encountered on collecting trips ranged from 27.8 to 33.8 ppt and temperatures from 8° C to 15° C.

Sex ratios were determined by boiling the specimens and then removing them from the shells. In neogastropods sex can be easily determined by the presence or absence of the penis on the right side just behind the head. In some instances sexing was done on live individuals placed upside down in an aquarium. As the animal emerged to

right itself, the presence or absence of the penis was readily observable. This method was of limited use because of the tendency of animals to remain upside down for several hours before attempting to right themselves. In one instance a specimen of *Fasciolaria hunteria* remained overturned for more than 12 hours before finally righting itself.

Radulae were prepared in a manner modified from the methods presented by MAGELHAES (1948) and MAHONEY (1966). After an animal was removed from the shell the proboscis was dissected out and placed in a concentrated aqueous solution of sodium hydroxide for several hours. The radula was then transferred to a fresh solution of sodium hydroxide to remove any remaining tissues, flattened between 2 slides, which were bound together, and allowed to dehydrate in 70% ethanol for 10 minutes. The radula was immersed in solutions of 5% oxalic acid and 1% potassium permanganate for 5 minutes each, then stained in Orange-G. The radula was then dehydrated completely, cleared in xylene and mounted in Euparal.

#### PHYSICAL DESCRIPTION OF ALLIGATOR HARBOR

Alligator Harbor on the northwest coast of Florida is bounded on the north by the mainland and on the south by Alligator Point, which has a continuous land connec-



Figure 1  
Map of Alligator Harbor



Figure 2

Photograph of shells of *Fasciolaria hunteria* (right) and *Fasciolaria tulipa* (left). Scale nearest the shells is in inches





tion with the mainland at the east end of the harbor (Figure 1). The marine laboratory of the Florida State University was located at Alligator Harbor for many years, but has recently been moved 8 miles west to Turkey Point. Alligator Harbor is a neutral estuary 4 miles long and  $1\frac{1}{4}$  miles wide with no major rivers or streams entering the harbor to dilute the sea water (OLSON, 1955). Salinities seldom vary by more than 3 ppt over the entire harbor surface, and normally range between 30 and 34 ppt. Although greater fluctuations are not uncommon, there are no known seasonal or annual variations in salinity. Many of the salinity variations that do occur are attributed to tidal mixing of harbor water with the adjacent Gulf water (OLSEN, *op. cit.*).

Alligator Harbor is uniformly shallow with an average depth of 1.2m and a maximum depth of 3m at mean low water, except for one hole with a depth approaching 6m. Although the normal tidal range is only 0.58m, the vertical distance between high and low water levels may approach 2m on some spring tides.

Despite its small size and the lack of significant fresh-water inflows, Alligator Harbor offers several types of habitats. The harbor bottom is composed of sand or sandy mud. Salt marshes with localized oyster reefs occurring in the east end of the harbor are drained by two small tidal creeks and their tributaries. The oyster reefs are found primarily along the edges of the salt marshes and the mouths of the tidal creeks, and extend from slightly above mean low water to about  $\frac{1}{2}$ m above mean low water (NICHY 1957). Most of the oysters in Alligator Harbor are *Crassostrea virginica* with a mean length of 50 - 60 millimeters. Oysters are also found adjacent to the docks of the old Florida State University marine laboratory.

Alligator Harbor is bordered by sandy beaches interspersed with muddy areas. The harbor mouth is closed by Bay Mouth Bar, a typical sand bar, except for natural channels at St. Teresa and Alligator Point. Although Bay Mouth Bar is completely submerged at high tide, substantial portions largely overgrown with *Thalassia testudinum* and *Diplantheria wrightii* are uncovered at low tide. The bar supports a diversified fauna which includes at least 40 species of mollusks.

## OBSERVATIONS

### Shell Anatomy

**General Shape:** To conduct an ecological study of this type, one must be able to recognize the species being studied and become aware of traits that reflect adaptations to different niches. For this reason, a detailed analysis of the shells of *Fasciolaria hunteria* and *F. tulipa* was

made. As can be seen in Figure 2, <sup>(E)</sup> the shells of both *F. hunteria* and *F. tulipa* are fusiform with moderately long anterior siphonal canals. Both species are dextral and remarkably similar in shape. Shells of young individuals of the two species resemble each other so closely that they cannot be distinguished by any characteristic other than coloration.

There is a marked difference in the maximum size of *Fasciolaria hunteria* and *F. tulipa*, but growth rates are not known for either species. A sample of 206 individuals of *F. hunteria* had an average length of 59.3 mm, with the largest being 85.5 mm (Table 1). ABBOTT (1954) reported

Table 1

Comparison of Shell Dimensions of  
*Fasciolaria hunteria* and *Fasciolaria tulipa*

Characteristic	<i>Fasciolaria hunteria</i>	<i>Fasciolaria tulipa</i>
Shell Length:		
Number of specimens	206	39
Maximum length (mm)	85.5	148
Minimum length (mm)	34.8	107.4
Mean length (mm)	59.3	128
Shell Width:		
Number of specimens	71	39
Maximum width	40.0	72.8
Minimum width	22.8	50.2
Mean width	29.3	59.6
Length to Width Ratio		
Number of specimens	71	39
Maximum L/W ratio	2.16	2.23
Minimum L/W ratio	1.78	1.91
Mean L/W ratio	1.94	2.07
Operculum Dimensions:		
Number of specimens	38	11
Mean operculum length	24.3	61.7
Mean operculum width	11.4	27.9
Mean operculum length to shell length ratio	0.45	0.44

the length of *F. hunteria* as 50 to 100 mm. WELLS (1958) used specimens ranging in size from 47 to 103 mm, with most individuals measuring between 75 and 90 mm in length. The maximum lengths reported by ABBOTT and

<sup>(E)</sup> Editor's note: Figure numbers in *Italics* refer to illustrations on halftone plates, whereas Roman numbers refer to illustrations in the text.

WELLS are much greater than the maximum found in the local population. JOHNSON (1919) recorded the length of *F. hunteria* as 65 to 85 mm, which is similar to the lengths obtained for the Alligator Harbor population. Thirty-nine adult individuals of *F. tulipa* averaged 128.4 mm in length, with the largest specimen measuring 162 mm. This exceeds the length of 75 to 125 mm given by ABBOTT (*op. cit.*), but is much smaller than the maximum of 200 mm reported by JOHNSON (*op. cit.*). As could be expected, the shells differ in thickness. Shells of adult *F. hunteria* average 0.3 mm, while the larger *F. tulipa* shells average 0.5 mm in thickness at the lip. Immature specimens of *F. tulipa* have the same thickness as shells of *F. hunteria* of the same size.

**Sculpturing:** Growth lines are not easily distinguished, especially in younger individuals, and both species are completely lacking in shell spines. *Fasciolaria hunteria* has 4 to 8 primary black lines on the body whorl that are secreted by correspondingly lined tissues on the underlying mantle. This is more variable than was indicated by either JOHNSON (1919) or HOLLISTER (1957). The latter reported that there are 6 primary spiral lines, while the former reported 5 or 6, which is in accord with the findings of the present study, accounting for 93% of the total number of individuals. Although the lines are equidistant in most cases, some lines on a few specimens are twice as far apart as the adjacent pairs of lines, indicating that one line was not formed. While only 2 primary lines re-

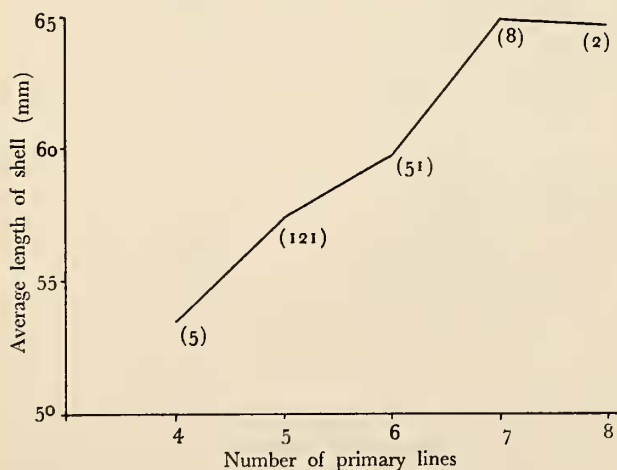


Figure 3

Graph of length of shell vs. number of primary lines in *Fasciolaria hunteria*. Numbers in parentheses indicate number of individuals

main visible in the early whorls, adults have the same number of primary lines as they had as juveniles. Many shells have secondary lines that are not continuous to the aperture and are not as fully formed as the primary lines. Adult individuals with more primary lines have a greater average length than individuals with fewer primary lines (Figure 3), which suggests that they were initially larger. The number of lines present in a juvenile individual cannot be used to accurately predict the adult size of the individual because of the significant overlap in the lengths of individuals with varying numbers of lines.

Shells of adult *Fasciolaria tulipa* have 25 to 39 spiral black lines which, unlike those of *F. hunteria*, are interrupted at frequent intervals. The first several lines near the body suture are grooved, but the remaining lines are not. Lack of shells with intermediate numbers of lines and the poor condition of many due to encrustations prevented any correlation between the number of lines and the length of shell being made in *F. tulipa*. The lines of adult *F. tulipa* extend on small teeth past the lip margin, giving the lip a notched appearance (Table 2).

Five to 8 ribs are found on the siphonal canal of *Fasciolaria hunteria* just below the primary lines; 15 to 20 ribs are present over the siphonal canal of *F. tulipa*, and there are about 75 small ribs on the inner surface of the lip of adult individuals of both species. A ridge on the

Table 2

Comparison of Shells of *Fasciolaria hunteria* and *Fasciolaria tulipa* from Alligator Harbor

Description	<i>Fasciolaria hunteria</i>	<i>Fasciolaria tulipa</i>
Thickness of shell (mm)	0.3	0.5
Primary lines	4-8	25-39
Character of lines	Solid	Interrupted
Lines extend on ridges	No	Yes
Siphonal ribs	5-8	15-20
Ridge for anal canal	Present	Absent
First lines grooved	No	Yes
Primary color	Gray	Brown

body whorl just under the shoulder of *F. hunteria* forms one side of a groove containing the anal canal (HOLLISTER, 1957).

**Coloration:** Differences in the color of the shells of *Fasciolaria hunteria* and *F. tulipa* are readily noticed. The background color of both the lip and the whorl is whitish

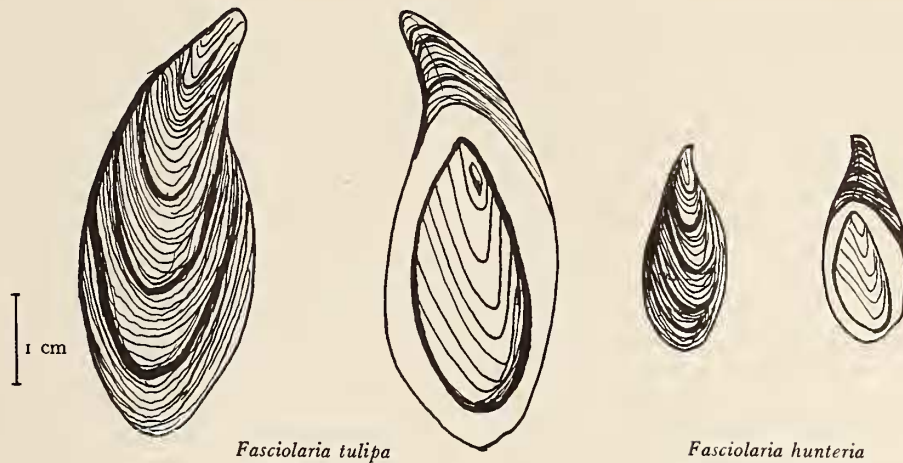


Figure 4

Comparison of the opercula of *Fasciolaria hunteria* and *Fasciolaria tulipa*

in both species. The presence of black spiral lines has already been mentioned. Shells of *F. hunteria* are blotched with gray, while those of *F. tulipa* are splotched with brown, and are often covered with encrustations. ABBOTT (1954) mentioned a rare albino form of *F. hunteria* and a mahogany variety of *F. tulipa*, but neither was encountered in this study.

**Periostracum and Operculum:** The brown periostracum of both species is so thin that its presence is not easily determined, especially in *Fasciolaria tulipa* when the shell is encrusted. The uncalcified operculum is secreted by and borne on the dorsal surface of the metapodium (HYMAN, 1968). The opercula are pointed anteriorly and rounded posteriorly (Figure 4), with different patterns on the dorsal and ventral surface of each operculum. The ventral side of the operculum has a large muscle scar where it is attached to the foot, whereas the margin of the operculum remains free and unattached to the foot. Growth lines are readily seen on the modified concentric pattern of the

operculum. The operculum serves a protective function by completely closing the aperture when the animal retreats into its shell. The operculum can also be used as a weapon. HOLLISTER (1957) reported that it functions as a claw, but did not describe how this is done. The present author found that the animal often extends itself completely when being held in the hand. A rapid contraction of the foot can bring the pointed anterior end of the operculum into sharp contact with the unsuspecting hand, causing the shell to be dropped. RANDALL (1964) noticed a similar defense mechanism in the queen conch, *Strombus gigas* LINNAEUS, 1758.

### Radulae

Radulae vary widely among the various groups of proso-branches, and are consequently of great taxonomic importance. HOLLISTER (1954) demonstrated a direct correla-



Figure 5

Radular teeth of *Fasciolaria*



tion between the number of cusps on the lateral teeth of the radula and the size of the shell in *Fasciolaria tulipa* and *F. gigantea* (= *Pleuroploca gigantea*). He also showed that at any particular size, *F. tulipa* has a larger number of cusps on the lateral teeth. The number of these cusps also increases with the length of the shell in *Busycon carica* GMELIN, 1791, and *B. contrarium* CONRAD, 1867, but the increase is not as great as in *Fasciolaria* (HOLLISTER, 1954). Of the two species of *Busycon*, specimens of the same size have the same number of cusps on the lateral teeth.

The present author investigated the radulae of *Fasciolaria hunteria* and *F. tulipa* in order to better understand the feeding habits of the two species. Like most neogastropods, the carnivorous *Fasciolaria* have a reduced number of radular teeth, with only a tricuspid central tooth flanked on each side by a lateral tooth (Figure 5). There are no marginal teeth. MAES (1966) reported sexual dimorphism in the central tooth of *Nassa*. The 3 cusps of the central tooth of *Nassa* are of the same size in the female, but the central cusp is elongated in the male and dominates the tooth. No dimorphism of this type was found in either *F. hunteria* or *F. tulipa*.

The lateral teeth of *Fasciolaria hunteria* have between 8 and 17 cusps; those of *F. tulipa* have 15 to 34 cusps in the adult. The radular formula of a typical adult *F. hunteria* is 0.16/1.3/1.16/1.0 and that of an adult *F. tulipa* is 0.30/1.3/1.30/1.0. The number of lateral cusps increases directly with the length of the shell in a straight line relation in each species (Figure 6), not a curved one as HOLLISTER (1954) indicated on his graph

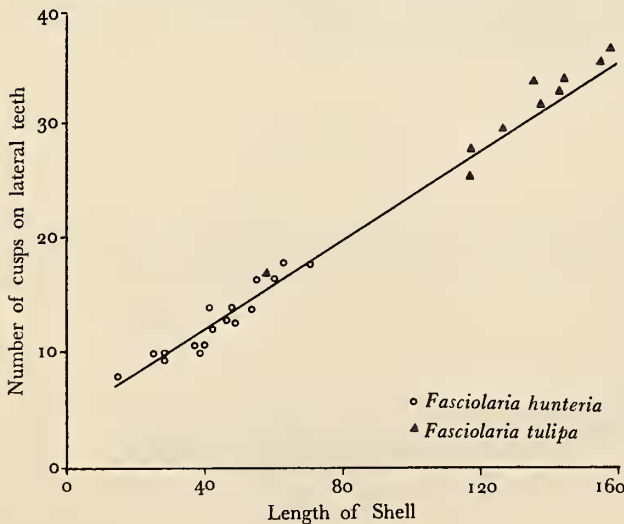


Figure 6

Graph of length of shell vs. number of cusps on the lateral teeth

for *F. tulipa*. Individuals 120 mm long have about twice as many cusps on the lateral teeth as those individuals 60 mm long. There is some variation in the number of cusps found in individuals of a given size, as is indicated on Figure 5. MAES (1967) reported a similar phenomenon in *Pleuroploca*, and found that individuals with thicker shells have more cusps than individuals of equal size with thinner shells. Thus, at a given size older individuals have more cusps on the lateral teeth than the younger individuals (MAYES, *op. cit.*).

The total number of teeth on a radula of an adult *Fasciolaria hunteria* varies from 225 to 265, while the larger *F. tulipa* has 300 to 350 teeth. This is similar to the 270 - 450 radular teeth reported for 3 species of *Busycon* (MAGALHAES, 1948). *Busycon* is a large carnivorous gastropod related to the Fasciolariidae, so the close parallel between the number of teeth in *Busycon* and *Fasciolaria* is not unexpected.

A bifurcation in the lateral cusp of a *Fasciolaria hunteria* was found. A similar abnormality was reported by MAGALHAES (1948) in one of the *Busycon* radulae studied. In most cases the number of cusps on the lateral teeth opposite a given central tooth are equal, but in some instances one of the lateral teeth has one more cusp than its opposite member.

Because it has been difficult to study a radula in a living animal, conclusions on radular growth must be drawn from preserved radulae. The teeth are formed in a radular sac and move forward to replace the old teeth as they are worn away. The radula also increases in both length and width as the animal grows. The medial cusp of the lateral tooth is the largest (Figure 5), and the most lateral cusp is the smallest of the cusps on the tooth. In no case has an intermediately placed cusp been larger than the medial cusp. MAES (1967) found that the additional cusps of the lateral teeth in *Pleuroploca* are added at the margin. As the radula moves forward the new cusps that are formed become progressively larger until the cusp has reached full size and new cusps have been formed along the margin of the radula.

#### Distribution of *Fasciolaria* in Alligator Harbor

As can be seen in Figure 7, *Fasciolaria hunteria* occurs in small groups along the margins of Alligator Harbor, from Bay Mouth Bar in the west to Harbor Head Oyster Bar in the east in association with the oyster bars. As a result, the local distribution of *F. hunteria* is spotty (Figure 7). There are many areas in the harbor where *F. hunteria* does not occur since, with the exception of Bay Mouth Bar, this species is found in Alligator Harbor only in areas immediately adjacent to oyster reefs, and has not been



found on the sandy patches between oyster clumps. Most of the oysters in Alligator Harbor are found on piers, concrete walls, or other artificial substrata along the margins of the harbor, and at the reef at the east end of the harbor. Since the southern portion of the harbor has been most modified by man, most of the habitats suitable for *F. hunteria* occur there. Of 50 individuals collected in a survey of the piers of the old marine laboratory, 46% were on oysters, 42% were within 30 cm of the nearest oyster, and only 12% were more than 30 cm from the nearest oyster. The maximum distance separating *F. hunteria* from the adjacent oysters was 180 cm. Many of the oyster reefs in Alligator Harbor are found at the harbor head, but it is interesting to note that *F. hunteria* is rare in that area despite its affinity for oysters. A possible explanation is that *Urosalpinx perrugata* CONRAD, 1846, a principal food of *F. hunteria* on oyster reefs, is lacking in the harbor head area, but it is also possible that the factor preventing *Urosalpinx* from getting a foothold there also keeps *F. hunteria* out.

Living specimens of *Fasciolaria tulipa* in Alligator Harbor were found only on Bay Mouth Bar, except for 2 individuals found in a grass flat on the north shore. Dead shells were found near the docks of the old marine laboratory, near the Harbor Head Oyster Bar, and near the piers along the southern margin of the harbor, but extensive investigations of these areas have not revealed a single living individual, so it appears likely that the shells were introduced into these areas after the animals died. *Fasciolaria tulipa* is widely distributed in the subtidal areas surrounding Bay Mouth Bar and the waters off St.

Teresa, as was evidenced in collections made on snorkeling trips to those areas. *Fasciolaria tulipa* is found in association with beds of *Diplantheria* and *Thalassia*. Neither plant species forms beds in the harbor itself.

Bay Mouth Bar is the only area of Alligator Harbor where *Fasciolaria hunteria* and *F. tulipa* are truly sympatric. About 80% of the *F. hunteria* collected on the bar came from the sandy areas of the southern end. *Fasciolaria tulipa* is distributed throughout the grass beds that cover most of the bar, but does not occur in the sandy areas. *Fasciolaria tulipa* and *F. hunteria* have been found as close as 5 feet apart on the grass flats.

### Population Characteristics

ANDREWARTHA & BIRCH (1954) described 3 conditions necessary for successful mark and recapture experiments. The marked individuals must be distributed homogeneously among the unmarked individuals of the population such that the marked specimens are not clumped together in a small portion of the study area. The marked individuals must have the same chance of being recaptured as the unmarked individuals, and there must be no movement of the population to or from the study area. Individuals of *Fasciolaria hunteria* found at the old marine laboratory and on Bay Mouth Bar were marked with notches on the lip of the shell. Recaptures were not attempted until at least one week after marking to allow the marked individuals to distribute themselves throughout the population. Since there was no way to observe the marking until the snail was in the collector's hand, marked



Figure 7

Distribution of *Fasciolaria* in Alligator Harbor

animals had the same chance of being collected as the unmarked ones. Because no marked individuals were found in areas other than the one in which releases were made, it appears that *F. hunteria* limits its movement to the area immediately adjacent to the oyster reef on which it lives. Most individuals of *F. hunteria* living along a concrete wall 600 m from the marine laboratory were removed in July, 1968. Despite the relative proximity of the marine laboratory population, no repopulation of the wall had occurred by April 1969. The tendency of individuals to remain in a small home area is not due to an inability of *F. hunteria* to traverse the sandy areas between oyster outcrops because this species has been observed to move forward at a rate of up to 10 cm/minute on sand by means of retrograde monotaxic muscular waves on the sole of the foot.

If  $P$  is the population size in number of individuals,  $M$  the number of marked individuals,  $N$  the total number of individuals subsequently recaptured and  $R$  the number of marked individuals recovered, then  $P = NM/R$  (ANDREAWARTHA & BIRCH, 1954). Using this formula for obtaining population size, the marine laboratory population of *F. hunteria* was estimated at 132 individuals, and the Bay Mouth Bar population at 720 individuals. The estimates were based on a small number of returns, and more work would have to be done to establish a better estimate. The lack of recaptures is a problem often encountered in mark and recapture experiments.

The relatively small number of *Fasciolaria tulipa* present on Bay Mouth Bar prevented a mark and recapture experiment on this species. The population density of *F. tulipa* was determined in the manner described by NICHY (1956). The investigator walked in a straight line and recorded the number of individuals found within reach of either arm. Thus, a corridor was made along the bar, and the number of individuals encountered divided by the length of the corridor gave an estimate of the density of the population. A small error was introduced by the inability of the investigator to locate buried specimens. The density of the *F. tulipa* population on the bar in early March was estimated at 0.0011 individuals per square meter, or one *F. tulipa* for every 917 m<sup>2</sup> on the bar surface. The population on the bar was just beginning to increase from the winter low when the estimate was made. According to the graph of the relative population sizes of snails on Bay Mouth Bar over the year presented by PAINE (1963), the density of the *F. tulipa* population would be expected to increase to 3 or 4 times the density in March by early summer.

The age distribution of the members of a population is an important characteristic influencing both natality and mortality (ODUM, 1953). A rapidly expanding population has a larger proportion of younger individuals than

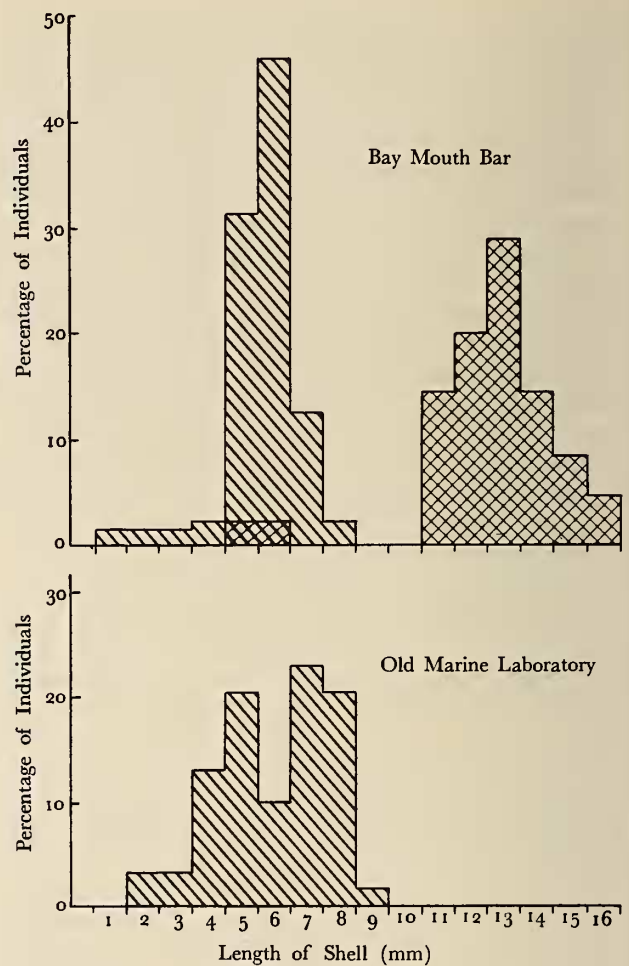


Figure 8

Graph of length of shell vs. percentage of individuals in population  
Graphs at left are for *Fasciolaria hunteria*; graph at upper right is  
for *Fasciolaria tulipa*

an older one. Figure 8 is a graph of the length vs. frequency of individuals from the populations on Bay Mouth Bar and at the old marine laboratory. There are very few small individuals of either *Fasciolaria hunteria* or *F. tulipa*, indicating that the populations are static. The smaller specimens are found in protected areas such as old shells, or between the valves of the pen shell, *Atrina*. The young often feed on the remains of dead *Atrina* and the tidbits left on the inside of the valves of the bay scallop *Aequipecten irradians* (LAMARCK, 1847) after a predator has eaten most of the bivalve and abandoned the prey.

In his paper on trophic relations on Bay Mouth Bar, PAINE (1963) presented graphs of the frequency of sev-



eral size classes of both *Fasciolaria hunteria* and *F. tulipa*, but the graphs are not as detailed as Figure 8. The general outlines of PAINE's graphs indicate that the *Fasciolaria* populations have remained fairly stable since PAINE studied the bar in 1959 and 1960. A major difference in the 2 sets of graphs is the lack of extremely large individuals of both species on the bar now compared to the number present in 1960. Although PAINE studied the bar over an entire year, the differences in the graphs are not due to differences in the time of year at which they were made. The lack of large individuals may be due to the activity of collectors, who generally select the largest specimens available. The population of *F. hunteria* at the marine laboratory is similar in structure to the Bay Mouth Bar population, but there is a somewhat larger proportion of extremely large individuals and of very small ones.

### Sexual Characteristics

**Mating Habits:** I observed the mating position of both species of *Fasciolaria* on numerous occasions. The female lies passively in the sand with her body in the normal upright position (Figure 9). The male is upside down with the axis of his shell almost at right angles to that of the female. Using his foot as a lever, the male presses his

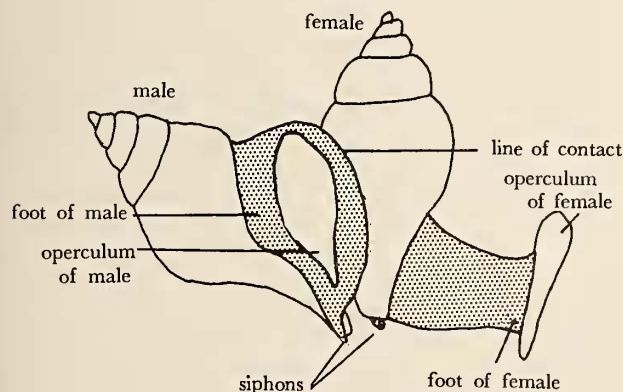


Figure 9

Mating position of *Fasciolaria*, viewed from above

shell into close contact with the female in such a way that there is a slight overlap of the shells in the outer lip area. In this position the siphonal canals are oriented in almost the same direction except that the siphonal canal of the male is inverted. With the 2 individuals in this position the

male is able to insert his penis into the vagina of the female.

The mating position is maintained for periods of up to 125 minutes, during which neither snail moves. HATHAWAY (1957) reported that *Melongena corona* GMELIN, 1791, which has a similar mating stance, remained in copulation for 90 to 100 minutes. A mating pair of *Fasciolaria hunteria* was placed in a glass fingerbowl to facilitate study. The transfer had little effect on either individual, and the mating position was maintained. After 50 minutes the female extended her foot in preparation for crawling and became generally active at the termination of mating. Separation was rapid and complete, after which the female crawled away while the male regained his normal crawling position.

A total of 25 matings of *Fasciolaria hunteria* and 4 of *F. tulipa* was observed in the field and in the laboratory during the study period. Individuals of both sexes of both species mated up to 3 times during a single week, indicating that individuals may mate more than once in a season. Animals were observed mating in the field during both day and night hours from the end of January until observations were terminated at the end of March. Some of the pairs were observed mating subtidally, but the majority was uncovered by the receding tides. Although both species normally burrow into the substratum when the falling tides expose them, those uncovered during copulation do not terminate their mating to seek refuge in the sand.

**Sexual Dimorphism of the Shell:** During this study a total of 151 specimens of *Fasciolaria hunteria* was sexed and measured to determine the sex ratio and to investigate the possibility of sexual dimorphism in shell length. Females of *F. hunteria* averaged 60.4 mm long, while males measured 57.6 mm, but despite the consistency of the difference in the various samples, statistical tests revealed no significant difference in the average lengths of the male and female shells.

Males of *Fasciolaria tulipa* averaged 124.0 mm in length, while the females had a mean length of 145.3 mm. This difference is statistically significant ( $p < 0.001$ ), revealing a sexual dimorphism in the length of the shells of *F. tulipa*.

**Sex Ratios:** Of the 151 specimens of *Fasciolaria hunteria* sexed, 47% were females and 53% were males. Sex ratios of the samples therefore approximated the 1:1 ratio, except for one sample at the old marine laboratory that had 1 female and 8 males. Samples taken at the same location before and after the aberrant sample all approximated the expected proportion of half male and half



female. The sex ratio for 18 individuals of *F. tulipa* collected during the study was exactly 1:1.

### Activity Rhythms

*Fasciolaria hunteria* is primarily a nocturnal species, although a few individuals can be found on the sand during the daytime. Several collecting trips were made to the old marine laboratory at different hours to gather the data presented in Figure 10. Weather, tidal, and water con-

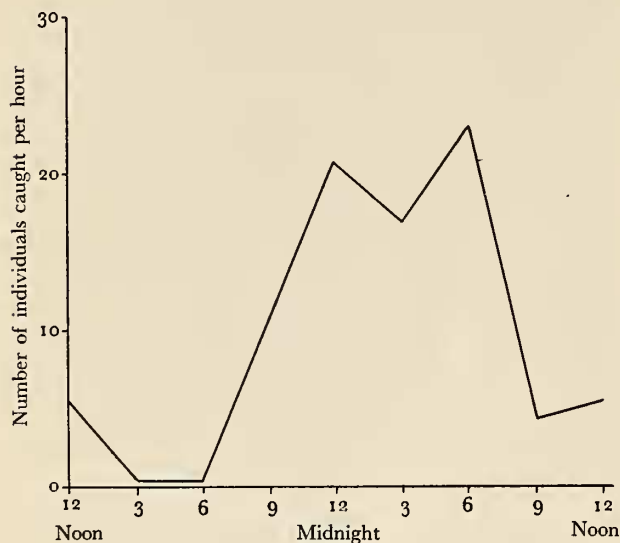


Figure 10

Number of *Fasciolaria hunteria* caught per hour at the old Marine Laboratory

ditions were similar on the various trips, and animals encountered were left in their habitat so that the number of individuals found on later trips was not lessened by earlier removal of part of the population. The number of specimens collected per hour averaged 16.7 for the night trips and only 2.4 for the day trips. Most of the snails collected at night were on oysters, actively feeding, or copulating. Individuals found during the day were invariably partially buried in the sand with the upper portions of the shell visible.

**Tidal Rhythm:** *Fasciolaria hunteria* frequently climbs piers and searches for food among the attached oysters when the tide is in. Individuals exposed to the air as the water level drops fall from the oysters to the sand below and burrow into the substratum. *Fasciolaria hun-*

*teria* on Bay Mouth Bar also burrow into the sand as the receding tide exposes them. In both areas there are a few individuals that remain above the sand after the tide has receded. Snails below the tide level, and those in the tide pools, are not exposed to the air and remain active throughout the low tide period at night, but individuals of this species are not active during the day. Copulating pairs ignore the exposure and continue mating. As the tide returns, the sand containing the burrowed snails is again under water and the animals rapidly emerge and resume their normal activity.

*Fasciolaria tulipa* is widely distributed in the subtidal areas adjacent to Bay Mouth Bar, and has been collected in waters up to 10 feet deep. This larger species is not normally subject to frequent tidal exposure and tends to have a much more uniform activity pattern than *F. hunteria*. None of the animals found subtidally was even partially buried in the substratum, and all were actively moving or feeding. The number of individuals exposed by minus tides on Bay Mouth Bar is quite small when compared to the population as a whole, but when *F. tulipa* is exposed, it also burrows into the sand.

**Seasonal Rhythms:** PAINE (1963) found *Fasciolaria hunteria* to be present on Bay Mouth Bar at all times of the year. The populations within the harbor are also present at all times, and are not subject to wide seasonal variations. *Fasciolaria tulipa* is present on Bay Mouth Bar in large numbers during the spring, but the numbers decline by August (PAINE, *op. cit.*). PAINE attributed the decrease in the number of *F. tulipa* on the bar to an increase in the number of predatory *Pleuroploca gigantea*. Only isolated individuals of *F. tulipa* are found on Bay Mouth Bar during the winter months.

### Predators and Escape Responses

PAINE (1963) reported that both *Fasciolaria hunteria* and *F. tulipa* are tertiary consumers and are at the top of the food web at Bay Mouth Bar. In this position *Fasciolaria* is relatively free of predators. PAINE found *F. tulipa* to be cannibalistic; similarly, I found *F. hunteria* to prey on members of its own species. The large gastropod *Pleuroploca gigantea* feeds on the 2 species of *Fasciolaria* (PAINE, 1963b), a process requiring a long period of time. Under aquarium conditions, one *P. gigantea* 11.9 cm took over 30 hours to consume a specimen of *F. hunteria* 5.8 cm long. *Murex fulvescens* SOWERBY and *Melongena corona* both feed on *F. hunteria*, but do not normally occur in the same habitat as *F. hunteria*.

SHOUP (1968) reported that both *Fasciolaria* species are consumed by crabs of the genus *Calappa*, and shells with the distinctive breakage pattern have been found in

Alligator Harbor. The stone crab *Menippe mercenaria* (SAY, 1818) is a predator of *F. hunteria* in oyster environments and on Bay Mouth Bar. One individual of *Pagurus pollicaris* SAY, 1817, was observed attacking a *F. hunteria* in the field, but the attack was not repeated in the laboratory.

Sting rays weighing up to 40 pounds are common in Alligator Harbor during the summer, but are absent during the winter months. The rays, which feed to a large extent on mollusks, appear to be major predators of *Fasciolaria* on Bay Mouth Bar.

Three types of defensive reactions are demonstrated by *Fasciolaria hunteria* upon encountering an individual of *F. tulipa*: withdrawal into the shell, active avoidance, and a flipping motion that is a modification of the righting response. GORE (1966) found a similar escape response pattern in *Nassarius vibex* SAY, 1817, elicited by *F. hunteria*, *F. tulipa* and the sea star *Luidia alternata* SAY, 1817. Withdrawal into the shell by *Fasciolaria* can be elicited by a variety of mechanical and visual stimuli. In both *F. hunteria* and *F. tulipa* the operculum completely seals off the aperture, preventing a predator from reaching the animal inside.

*Fasciolaria hunteria* exhibits the full spectrum of escape responses when stimulated by the presence of *F. tulipa* in the laboratory. Withdrawal into the shell has already been described. Four 10 to 15 gallon capacity aquaria were maintained in the laboratory, 2 with a 4-inch layer of sand on the bottom and 2 with a bare slate bottom. Individuals of both species were able to bury themselves completely in the sand. Ten *F. hunteria* were placed in tanks 1 and 2 with sandy bottoms, and 12 were placed in tanks 3 and 4 with the slate bottoms. Four *F. tulipa* were put in tank 2, and 3 were included in tank 4. The results of observations made over a 1-week period are given in Table

Table 3

The Position of *Fasciolaria hunteria* on the Walls of the Aquaria, on the Bottom, or Burrowed into the Sand in Relation to the Presence of *Fasciolaria tulipa*

Tank	Substratum	<i>Fasciolaria tulipa</i>	Percentage of <i>Fasciolaria hunteria</i>		
			on walls	on bottom	buried
1	Sand	0	22.4	24.0	53.6
2	Sand	4	3.5	2.0	94.5
3	Slate	0	1.0	99.0	-
4	Slate	2	83.6	16.4	-

3. No difference was found between data collected during the day and at night. *Fasciolaria tulipa* remained on the bottom or burrowed into the sand, but rarely climbed the sides of the aquaria. The individuals of *F. hunteria* were on the bottom of tank 4 only 16.4% of the time, while those in tank 3, without *F. tulipa* on the bottom, were on the bottom 99% of the time. Since this difference was statistically significant, it was concluded that the climbing by *F. hunteria* was an avoidance response to the predatory *F. tulipa*. Similar results were obtained in the aquaria with sandy bottoms. While only 53.6% of the *F. hunteria* in tank 1 were buried, 94.5% of those in tank 2 burrowed into the sand. Almost  $\frac{2}{3}$  of the *F. hunteria* that did venture out of the sand in tank 2 climbed the sides of the aquarium in the avoidance response found in tank 4. In several instances *F. hunteria* that ventured too near *F. tulipa* were captured and eaten. From the data obtained, it appears that *F. hunteria* actively avoids *F. tulipa* by burrowing if a choice between burrowing and fleeing is present. If no choice is available the *F. hunteria* climbs the aquarium walls as an escape response from the predator.

The righting response of the 2 species of *Fasciolaria* is modified into the flipping escape response seen in *F. hunteria*. An understanding of the righting response will make the mechanics involved in the escape response easier to visualize. The righting action of both species may be divided into 3 sequential steps similar to those described by CLARK (1964). The overturned snail contracts the circular muscles of its foot, thrusting the foot outward from the columella. In 29 of the 31 righting responses witnessed, the foot was extended around the inner lip and the columella of the shell. In the remaining cases the foot was extended over the outer lip of the shell. Individuals unable to reach the substratum by the first method chosen made a second attempt from the other side of the shell.

Differences were observed in the righting responses taking place on a solid or sand substratum. A specimen of *Fasciolaria* on a solid surface extends the anterior portion of the foot until it contacts the substratum and creates a suction with the help of a mucous secretion. The longitudinal foot muscles contract to pull the shell over. The foot is unable to establish a firm grip on a sandy substratum, however, and in this situation the snail extends and twists the distal portion of its foot so that the pointed anterior tip of the operculum is facing the substratum. A rapid contraction of the foot muscles drives the operculum into the substratum where it serves as an anchor. When the longitudinal foot muscles contract, the shell is pulled over, rather than the foot being pulled loose.

The initial attempt at righting the shell was successful in 55% of the 31 rightings investigated, and 19% of the 31 rightings were successful on the second try. *Fasciolaria*



unable to right themselves after repeated attempts resort to a more active method. The foot is rapidly extended in the manner described, but when the substratum is reached the foot is quickly extended by a kicking motion, which often lifts the entire shell and body off the substratum and throws the animal a distance of 3 or 4 cm. This process is repeated until the animal happens to fall in the normal upright position.

A modification of the rapid righting response described above is used in the escape response of *Fasciolaria hunteria*. The flipping response is begun in the presence of *F. tulipa* and continues until the *F. hunteria* is some distance away. *Fasciolaria hunteria* in aquaria have been observed crawling about on the shells and opercula of *F. tulipa* without indicating an attempt to escape. However, a specimen of *F. hunteria* approaching the anterior portion of the foot of *F. tulipa* initiated the escape response before physical contact was made, indicating a possible chemical or visual mediation of the response. Individuals trapped beneath the foot of *F. tulipa* respond immediately and continue to flip until the 2 species are no longer in contact.

## DISCUSSION

The primary concern of this paper has been the investigation of the ecological similarities and differences of *Fasciolaria hunteria* and *F. tulipa*, and the manner in which these ecological characteristics reflect upon the theoretical problems arising from the sympatric distribution of these two morphologically and phylogenetically closely related species. CAIN (1953) limited the field of consideration of sympatry to an area in which the breeding ranges of the two species overlap. Although the two species of *Fasciolaria* share a wide geographical range, the area in which the two species are truly sympatric is limited, at least in Alligator Harbor.

*Fasciolaria hunteria* and *F. tulipa* are truly sympatric in Alligator Harbor only on Bay Mouth Bar. Since individuals of both species have been observed copulating on the bar at the same times of the year, their breeding ranges are also sympatric in this limited area, and there is no physical barrier to interbreeding. However, when the two species do come together *F. hunteria* is selectively eaten by *F. tulipa* (PAINE, 1963), unless an escape response is effective in removing the smaller tulip from contact with the larger *F. tulipa*. This would prevent crossbreeding from occurring when individuals of the two species encounter each other.

HARPER *et al.* (1961) found 3 factors to be necessary for the continued coexistence of closely related species. All species must be able to tolerate the physical and bio-

logical hazards of the environment. The related species must be able to maintain the genetic differences between them. HARPER *et al.* (*op. cit.*) also cited 3 genetic conditions which can result when closely related species coexist. First, the breeding behavior may prevent hybrids from being formed. In the second situation hybrids are produced by crossmatings, but the progeny is sterile. Finally, fertile hybrids result from crossmatings between the 2 species. The reproductive characteristics of the *Fasciolaria* populations in Alligator Harbor fit the first case. The 2 species are closely related: the shells are almost identical in shape and structure, the opercula are identical, and the structure of the radula in *F. hunteria* is not distinguishable from that of *F. tulipa* of the same size. Differences in coloration and size are the most important external distinguishing characteristics separating *F. hunteria* from *F. tulipa*. Although 30 mating pairs were observed, no interspecific matings were encountered in either the field or in the laboratory. No intermediate forms resembling hybrids were found among the 295 live individuals of *F. hunteria* or the 18 live individuals of *F. tulipa* collected during the study.

PAINE (1962) pointed out that to coexist, potential competitors each must utilize some aspect of the common environment more effectively than the other. PAINE (*op. cit.*) also noted that if this were not the case, competitive pressures would lead to the exclusion or encourage modification of the less well adapted species. Differences in distributional patterns, the fact that *Fasciolaria hunteria* is primarily intertidal in Alligator Harbor and *F. tulipa* is subtidal, and differences in daily activity patterns all lessen the contact and competition between the 2 species. HAIRSTON (1959) claimed that food is the only resource that 2 competing species cannot share. PAINE (1963) presented feeding data for *F. hunteria* and *F. tulipa*, and also (PAINE, 1962) reported a feeding diversification in 2 sympatric *Busycon* species on Bay Mouth Bar. A similar diversification in the feeding habits of *Fasciolaria* is evident from the feeding data reported in PAINE'S (1963) paper. Bivalves comprised about the same portion of the diet of the 2 species, with *F. hunteria* feeding on the smaller bivalves. The majority (58%) of the prey of *F. tulipa* encountered by PAINE was other gastropods, compared with only 13% for *F. hunteria*. Polychaete worms accounted for 41% of the diet of *F. hunteria*, but none was included in the feeding observations of *F. tulipa*. PAINE concluded that the feeding differences in the 2 *Fasciolaria* were due to the difference in size of the 2 species. While both species are catholic feeders, the ability of *F. tulipa* to attack and consume larger prey than *F. hunteria*, and the larger species' corresponding disinterest in small potential prey, results